MIMETIC SELECTION AND SUBSPECIFIC VARIATION IN THE SPICEBUSH SWALLOWTAIL *PAPILIO TROILUS* LINNAEUS (LEPIDOPTERA: PAPILIONIDAE)

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Butterfly color patterns are determined by the interaction of a number of selective factors. Among these are sexual selection (Magnus, 1957, 1963; Tinbergen et al., 1942; Silberglied and Taylor, 1973; Hafernik, 1982), selection for thermoregulatory efficiency (Watt, 1968), crypsis (Wickler, 1968), aposematic coloration (Rothschild, 1972) and mimicry (Brower, 1958a, b; Platt et al., 1971; Platt and Brower, 1968; Wickler, 1968; Punnett, 1915). Perhaps the most interesting phenomena involved with selection for various wing patterns are those resulting from predator avoidance strategies. This paper discusses one such factor, mimetic selection, and proposes a new role for it in influencing subspecific wing pattern variation in the spicebush swallowtail *Papilio troilus* Linnaeus.

The *Battus philenor* Mimicry Complex

Larvae of the pipevine swallowtail *Battus philenor* (Linnaeus) feed on leaves of *Aristolochia,* a genus known to contain substantial concentrations of toxic aristolochic acids (Rothschild et al., 1970; Euw et al., 1968). As a result adults of *B. philenor* are distasteful to at least two species of birds and presumably to a wide array of other vertebrates (Brower, 1958a; Platt et al., 1971). In the eastern United States *B. philenor* generally is recognized as the model for a series of palatable mimics. This Batesian association includes males and females of *P. troilus troilus,* females of *P. polyxenes* Fabricius, and the dark female form of *P. glaucus* Linnaeus (all Papilionidae); and two nymphalid butterflies *Limenitis arthemis astyanax* (Fabricius) and females of *Speyeria diana* (Cramer); as well as males of the saturniid moth *Callosamia promethia* (Drury) and related species (Brower and Brower, 1962; Waldbauer and Sternburg, 1975).

Battus philenor ranges from New England south into Central America but is absent or rare in Florida (Klots, 1951; Brower and Brower, 1962; Kimball, 1965). In the eastern United States most *B. philenor* mimics surpass the distribution of their model. Two of these *L. arthemis* (Drury) and *P. glaucus* show well-documented phenotypic variation correlated with increasing rarity or absence of *B. philenor* at the northern or southern limits of its distri-

bution (Platt and Brower, 1968; Burns, 1966). In the eastern United States, *L. arthemis* occurs as two subspecies: *L. a. astyanax,* which mimics *B. philenor,* and *L. a. arthemis,* which is disruptively colored. In New England and the Great Lakes States, as *B. philenor* becomes increasingly rare, selection apparently favors a switch from a mimetic strategy to one of camouflage (Platt and Brower, 1968). Similarly, north of the range of *B. philenor* mimetic females of *P. glaucus* are replaced by a disruptively colored form similar to the male in coloration (Platt and Brower, 1968; Burns, 1966). In southern Florida the frequency of mimetic morphs of *P. glaucus* is also reduced to six to eight per cent (Brower and Brower, 1962).

Battus polydamus as a Model for *Papilio troilus* in Florida

Nominate *P. troilus* is characterized by blue or greenish spots on the dorsal hindwing and small light spots on the dorsal forewing. This pattern is very similar to that of *B. philenor* (Fig. 1a, c). In Florida *P. troilus* greatly outnumbers *B. philenor,* its usual model further north. In fact, Brower and Brower (1962) found that the *troilus* to *philenor* ratio in southern Florida was about 1000 to 1 and that *B. philenor* was only slightly more common in northern Florida. In southern Georgia and northern Florida *P. t. troilus* intergrades with its floridian subspecies *P. t. ilioneus* Abbot and Smith, a butterfly characterized by a generally brighter, more yellowish green color pattern with well-developed forewing spots (Fig. 1d). As with *P. glaucus,* mentioned above, this switch in phenotypes parallels the decline in frequency of *B. philenor.*

Two hypotheses have been suggested to explain the switch over to the floridian phenotype in *P. troilus.* Brower and Brower (1962) suggest that the phenotypic change results from a relaxation of selection for a mimetic color pattern allowing the expression of deviant color patterns. This explanation would predict a similar deviation, although not necessarily in the same direction, in northern populations of *P. troilus* which exceed the range of their model, yet no such phenotypic change occurs in northern populations. Moreover, I believe it likely, as is apparently the case in *L. arthemis* and *P. glaucus,* that if selection for mimicry were relaxed other selective factors would increase in importance in determining color patterns. There is no indication that the *P. t. ilioneus* pattern is more cryptic than the *P. t. troilus* pattern nor have other selective reasons been suggested. The *ilioneus* phenotype is, if anything, more conspicuous than the normal morph and perhaps more easily spotted by predators.

The second explanation is that of Remington (1968) who believed that the *ilioneus* phenotype is the result of previous isolation of Florida *P. troilus* populations. Remington believed that a dense band of forest across northern Florida provided a barrier that until recently maintained geographic isolation
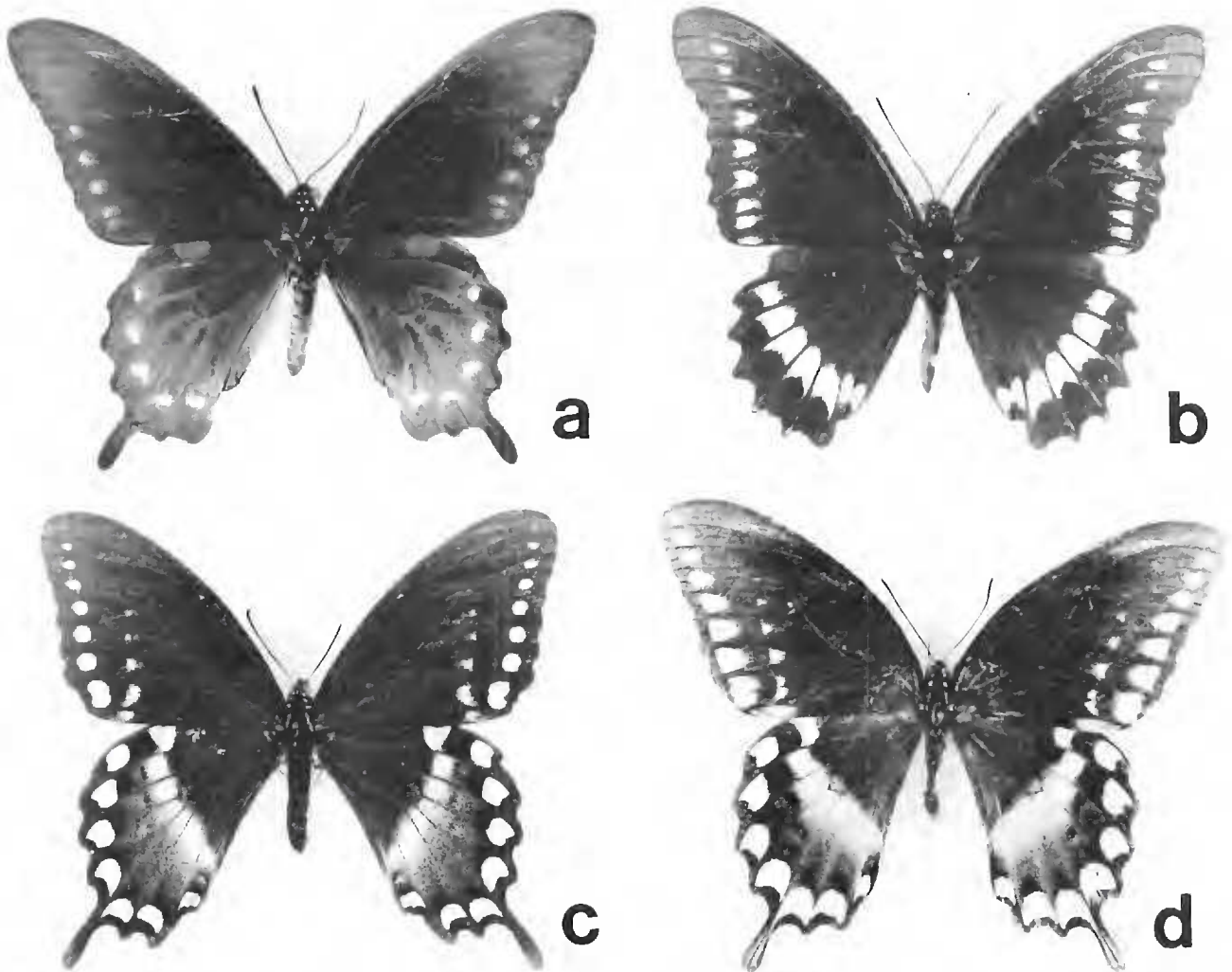
Fig. 1a–d. *Battus-Papilio troilus* mimicry complex. Fig. 1a, *Battus philenor,* St. Louis, Missouri. Fig. 1b, *Battus polydamus,* Sontecomapan, Veracruz, Mexico. Fig. 1c, *Papilio troilus troilus,* Bear Mountain, New York. Fig. 1d, *Papilio troilus ilioneus,* Lutz, Florida.

between the two subspecies. He explains the area of intergradation in northern Florida and southern Georgia as a region of secondary contact which may eventually result in the evolution of prezygotic isolating mechanisms between the two taxa. I do not find this scenario compelling since *P. troilus* is a forest butterfly (Klots, 1951; Emmel, 1975). It occurs commonly in such heavily forested areas as the Big Thicket area of east Texas (personal observation). This suggests that a dense forest would not significantly restrict gene flow between Florida and Georgia populations as it might have for other non-forest butterflies which show a similar distribution, but no evidence of subspecific differentiation.

In place of the above explanations, I propose a third, although not mutually exclusive, hypothesis. Study of spread specimens of *P. t. ilioneus* suggests the pattern of another *Aristolochia*-feeding swallowtail *B. polydamus* (Linnaeus) (Fig. 1b, d). Aristolochic acids have been isolated from the tissues of *B. polydamus* (Rothschild et al., 1970; Rothschild, 1972) and it is likely that

B. polydamus is unpalatable to a wide range of vertebrate predators although feeding trials have not been done. Waldbauer and Sternburg (1975) suggest that *B. polydamus* serves as the model for several Batesian mimics in the neotropics among them females of *Papilio androgeus* Cramer and *P. lyco-phron* Hübner. *Battus polydamus* is common in Florida and ranges north to southern Georgia where it is infrequent (Harris, 1972). No quantitative data are available on the relative proportions of *B. polydamus* and *P. troilus* in Florida. However, Kimball (1965) states that *B. polydamus* is at times more common than *P. troilus*. Thus there is circumstantial evidence that the change from the typical *troilus* morph to the *ilioneus* morph results from a change in frequency of suitable models.

Some workers group *P. troilus* populations in Texas and the Gulf States under the subspecies *ilioneus* (=*texanus* Ehrman) (Klots, 1951; Emmel, 1975). I am unable to distinguish differences among Texas populations and more northern *P. t. troilus*. *B. polydamus* occurs periodically in central and northern Texas and the Gulf States. If any tendencies toward *ilioneus*-like patterns exist in some populations, they could result from selection for patterns that provide mimetic advantage from both *B. philenor* and *B. polydamus*.

Discussion

The influence of availability and abundance of appropriate models on geographic variation of mimetic butterflies is well-known, especially for tropical species. Perhaps the best known and most intricate example of this kind of geographic pattern is that found in the African swallowtail *Papilio dardanus* Brown. This species occurs as a complex array of races whose females mimic several members of the unpalatable genera *Danaus* and *Amauris*. Frequencies of mimetic morphs are related to the abundance of particular models in each area (Clarke and Sheppard, 1960). In the United States subspecific variation in the well-known viceroy butterfly *Limenitis archippus* (Cramer) is also related to a change in abundance of models. Throughout most of its range *L. archippus* mimics the monarch *Danaus plexippus* (Linnaeus), but in the southwestern United States it mimics the related *D. gilippus strigosus* (Bates). In northern Florida and southern Georgia *L. archippus* populations switch from a *D. plexippus*-like pattern to one resembling *D. gilippus berenice* (Cramer). As pointed out by Remington (1968), this situation closely parallels the one outlined above for *Papilio troilus*.

The phenotypic similarity of *P. t. ilioneus* to *Battus polydamus,* the coincidence in range of the two, and the rarity of *B. philenor* in Florida offer strong circumstantial evidence of color pattern selection in Florida *P. troilus* for mimicry of *B. polydamus*. This explanation does not mutually exclude previous hypotheses. Indeed, the explanations of Remington (1968) and Brower and Brower (1962) may be partly correct. Previous isolation of

Florida *P. troilus,* as postulated by Remington, probably would have accelerated evolution of new color patterns using *B. polydamus* as a model. Furthermore, the absence of *B. philenor* from Florida, emphasized by Brower and Brower, would have been important in releasing *P. troilus* populations from stabilizing selection for *B. philenor*-like patterns.

Research into the following areas is needed to clarify the factors influencing variation among the southern populations of *P. troilus*: 1. Laboratory studies, of the type pioneered by the Brower group, utilizing caged predators in order to ascertain the unpalatability of *B. polydamus* and the efficiency of *P. troilus ilioneus vis-à-vis P. t. troilus* as a *B. polydamus* mimic. 2. Field studies of the relative abundance of *B. polydamus* and *P. troilus* in various parts of Florida and Georgia in conjunction with a quantitative analysis of geographic variation in *P. troilus* wing patterns in the southeastern United States.

Summary

The similarity in wing pattern of *Papilio troilus ilioneus* Abbot and Smith to that of *Battus polydamus* (Linnaeus), the coincidence in range of the two, and the rarity in Florida of *Battus philenor* (Linnaeus) the presumed model for *P. t. troilus* Linnaeus suggest that the *P. t. ilioneus* pattern is the result of selection for mimicry of *B. polydamus.* Previous explanations of the causes of subspecific variation in *P. troilus* are discussed in light of this new hypothesis.

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